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Authors: Brusatte, Stephen L., Benson, Roger B.J., and Xu, Xing

Source: Acta Palaeontologica Polonica, 57(1) : 65-72

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2010.0125

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A reassessment of *Kelmayisaurus petrolicus*, a large theropod dinosaur from the Early Cretaceous of China

STEPHEN L. BRUSATTE, ROGER B.J. BENSON, and XING XU



Brusatte, S.L., Benson, R.B.J., and Xu, X. 2012. A reassessment of *Kelmayisaurus petrolicus*, a large theropod dinosaur from the Early Cretaceous of China. *Acta Palaeontologica Polonica* 57 (1): 65–72.

The Early Cretaceous fossil record of large-bodied theropods from Asia is poor, hindering comparison of Asian predatory dinosaur faunas with those from other continents. One of the few large Asian theropod specimens from this interval is a partial skull (maxilla and dentary) from the Lianmugin Formation (?Valanginian–Albian), the holotype of *Kelmayisaurus petrolicus*. Most authors have either considered this specimen as an indeterminate basal tetanuran or a nomen dubium. We redescribe *K. petrolicus* and note that it possesses a single autapomorphy (a deep accessory groove on the lateral surface of the anterior dentary), as well as a unique combination of characters that differentiates it from other theropods, affirming its validity. A phylogenetic analysis recovers *K. petrolicus* as a basal carcharodontosaurid, which is supported by various features: very deep interdental plates (a carcharodontosaurid synapomorphy), fused interdental plates (present in carchardontosaurids and a limited number of other theropods), and the absence of diagnostic features of other clades of large-bodied theropods such as abelisaurids, megalosauroids, and coelurosaurs. As such, *Kelmayisaurus* is the second known carcharodontosaurid from Asia, and further evidence that this clade represented a global radiation of large-bodied predators during the Early–mid Cretaceous.

Key words: Dinosauria, Theropoda, Carcharodontosauridae, anatomy, Cretaceous, China.

Stephen L. Brusatte [sbrusatte@amnh.org], Division of Paleontology, American Museum of Natural History, Central Park West at 7'9th St., New York, NY, 10024, USA and Department of Earth and Environmental Sciences, Columbia University, New York, NY, USA;
Roger B.J. Benson [rbb27@cam.ac.uk], Department of Earth Sciences, UCL, University College London, Gower Street, London WC1E 6BT, UK; Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, UK;
Xing Xu [xingxu@vip.sina.com], Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, People's Republic of China.

Received 17 December 2010, accepted 7 April 2011, available online 28 April 2011.

Introduction

The fossil record of large-bodied theropod dinosaurs from the Early Cretaceous of Africa, Europe, North America, and South America has improved dramatically over the past two decades. Entirely new groups of distinctive theropods, including carcharodontosaurians, abelisaurids, and spinosaurids, have been discovered and now represent some of the best-known megapredators in the dinosaur fossil record (e.g., Bonaparte 1985; Charig and Milner 1997; Sereno et al. 1996; Benson et al. 2010). However, comparatively little is known about the large-bodied theropods that inhabited Asia during the Early–middle Cretaceous. Recent discoveries indicate that carcharodontosaurians (including both neovenatorids and carcharodontosaurids) and spinosaurids were present in the Early Cretaceous of Asia (Milner et al. 2007; Buffetaut et al. 2008; Brusatte et al. 2009a, 2010; Benson et al. 2010). Nevertheless, the large-bodied theropod record of Asia is poor, so single specimens can contribute to and potentially alter hypotheses of theropod biogeography and faunal change.

One of the few large-bodied theropod specimens from the Early Cretaceous of Asia is a partial skull, comprising a fragmentary maxilla and complete dentary, which was referred to a new genus and species, *Kelmayisaurus petrolicus*, by Dong (1973). Although fragmentary, this specimen was considered valid by Molnar et al. (1990) and Holtz et al. (2004), with the latter authors describing it as a basal tetanuran of uncertain affinities. However, in a review of small-bodied theropods from the Early Cretaceous of Asia, Rauhut and Xu (2005: 107) considered *Kelmayisaurus* to be a nomen dubium because of the "fragmentary nature of the type material and the lack of clearly diagnostic characters". Subsequently, this critical specimen from a poorly sampled interval has been ignored in discussions of Asian theropod anatomy, phylogeny, and evolution.

We redescribe the type specimen of *Kelmayisaurus*, providing for the first time a detailed anatomical description and comparison to other large theropod taxa. We present evidence that *Kelmayisaurus* is a valid taxon, diagnosable by a single autapomorphy as well as a unique combination of

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other characters. Furthermore, a phylogenetic analysis and comparisons with other theropods indicate that *Kelmayisaurus* is a member of Carcharodontosauridae, a clade of theropods that includes some of the largest predators to ever live and which was recently discovered in Asia for the first time (*Shaochilong maortuensis*: Brusatte et al. 2009a). Thus, *Kelmayisaurus* provides evidence that carcharodontosaurids were a long-lived component of Asian terrestrial ecosystems, and were a truly global radiation of hypercarnivorous (large-bodied, solely carnivorous) predators during the Early–mid Cretaceous.

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; DCM, Dorset County Museum, Dorchester, UK; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MUCP, Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén, Argentina; NCSM, North Carolina Museum of Natural Sciences, Raleigh, North Carolina; PVL, Instituto Miguel Lillo, Tucumán, Argentina; UMNH, Utah Museum of Natural History, Salt Lake City, Utah.

Systematic palaeontology

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Allosauroidea Marsh, 1878

Carcharodontosauria Benson, Carrano, and Brusatte, 2010

Carcharodontosauridae Stromer, 1931

Genus *Kelmayisaurus* Dong, 1973

Type species: *Kelmayisaurus petrolicus* Dong, 1973; see below.

Diagnosis.—Same as for the type and only known species.

Kelmayisaurus petrolicus Dong, 1973

Figs. 1, 2.

1973 *Kelmayisaurus petrolicus* Dong, 1973: fig 2: 4.
2008 *Kelmayisaurus petrolicus*; Zhao et al. 2008: fig. 323.

Holotype: IVPP V 4022, a complete left dentary and partial left maxilla.

Type locality: Near Wuerho (Urdo), Junggar Basin, Xinjiang, China (Shen and Mateer 1992; Rauhut and Xu 2005; Zhao et al. 2008).

Type horizon: Lianmugin Formation, Tugulu Group (Early Cretaceous: ?Valanginian–Albian).

Emended diagnosis.—Carcharodontosaurid with a single autapomorphy: the presence of a deeply inset and dorsally concave groove located anteriorly on the lateral surface of the dentary (Fig. $1B_1$). Additionally, *Kelmayisaurus* shows a unique combination of characters not currently known in any other allosauroid: maxillary interdental plates more than twice as tall dorsoventrally as they are broad anteroposteriorly, prominent maxillary anterior process (the combination of these two characters results in a narrowing of the gap between the plates and the anteromedial process), and absence of an anteroventral "chin-like" process of the dentary.

Description

Maxilla.—Only a small fragment of the left maxilla is present, comprising the region anterior to the base of the ascending process. A distinct anterior ramus is present, which is separated from the base of the ascending process by a concave step in lateral view. The shape of the ramus may have been slightly modified by breakage of the dorsal surface. However, neither cancellous bone texture nor alveolar crypts are exposed, suggesting that such breakage is minimal and the presence and general shape of the process are real. The anterior ramus is present in many basal theropods and its shape is often used as a phylogenetic character (e.g., Holtz et al. 2004). In *Kelmayisaurus* the process is slightly shorter anteroposteriorly (70 mm) than it is high dorsoventrally (100 mm), similar to the condition in *Allosaurus* (Madsen 1976), *Neovenator* (Brusatte et al. 2008), and *Monolophosaurus* (Brusatte et al. 2010; Zhao and Currie 1993). In contrast, carcharodontosaurids such as *Carcharodontosaurus* and *Mapusaurus* have an anterior process that is much taller than long anteroposteriorly, and thus is nearly indistinct as a discrete process (Sereno et al. 1996; Coria and Currie 2006).

The maxilla is heavily abraded but several regions of original bone surface are preserved. On the lateral surface, the best preserved patch of original surface texture is smooth, and lacks the rugose surface texture of abelisaurids (Sampson and Witmer 2007; Sereno and Brusatte 2008) and derived carcharodontosaurids such as *Carcharodontosaurus* (Sereno et al. 1996; Brusatte and Sereno 2007). Additionally, there is a row of primary neurovascular foramina approximately 15 mm above the ventral margin on the lateral surface. Where well preserved, the foramina are 4–5 mm in diameter and open ventrally into deep grooves that terminate at the alveolar margin. These grooves, along with other grooves on more abraded regions of the lateral surface, are marked by tightly packed and elongate internal bone grains. There are several larger foramina located dorsal to the primary row, but these do not appear to form a pattern.

The medial surface of the maxilla is poorly preserved, suggesting that it was exposed to subaerial weathering. However, important details of the interdental plates are apparent. Although the plates are damaged in many regions, it is clear that they were fused into a single lamina. Additionally, the first plate is preserved in its entirety; it extends dorsally to nearly the level of the anteromedial process and the two are only separated by a slight concave margin. This is also the case in *Sinraptor* (Currie and Zhao 1993). However, in *Sinraptor* this results from the more ventral position of the anteromedial process, whereas in *Kelmayisaurus* the process is located close to the dorsal margin of the maxilla as in most theropods. Thus, the close position of the first interdental plate and the anteromedial process in *Kelmayisaurus* is due to the increased depth of the plate itself. It is approximately twice as deep dorsoventrally as broad anteroposteriorly, as in derived carcharo-

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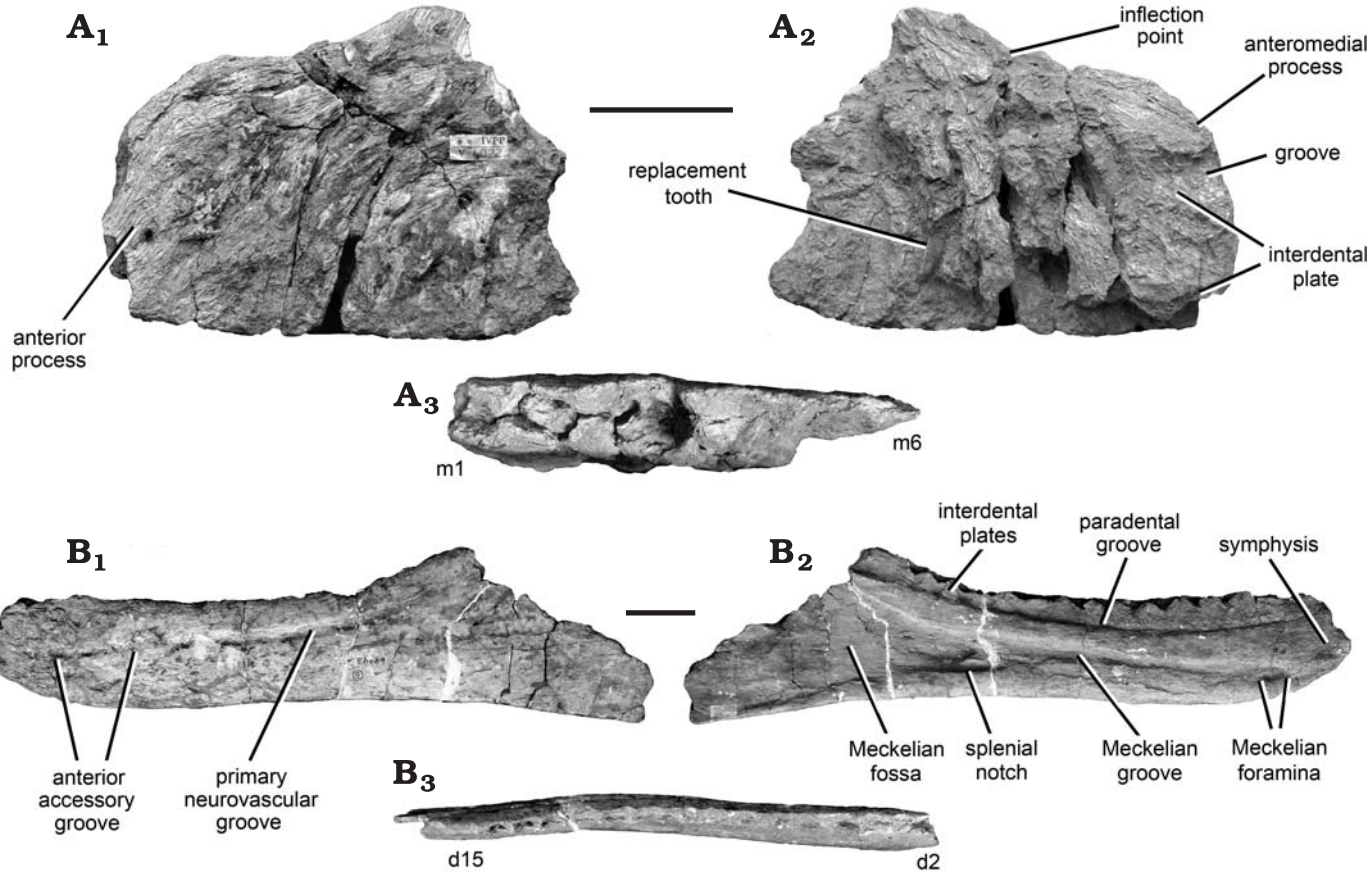


Fig. 1. Left maxilla (**A**) and left dentary (**B**) of carcharodontosaurid theropod *Kelmayisaurus petrolicus* Dong, 1973 (IVPP V 4022, China, Lianmugin Formation, Lower Cretaceous). Photographs in lateral (A_1, B_1), medial (A_2, B_2), ventral (A_3), and dorsal (B_3) views. Scale bars 5 cm. Designation "d" refers to dentary tooth, designation "m" refers to maxillary tooth position. Dorsal view of dentary shows tooth row only.

dontosaurids such as *Acrocanthosaurus* (NCSM 14345), *Carcharodontosaurus* (Brusatte and Sereno 2007), *Giganotosaurus* (MUCPv-Ch 1), and *Mapusaurus* (Coria and Currie 2006), as well as the megalosaurids *Megalosaurus* (Benson 2010) and *Torvosaurus* (Britt 1991) and specimens of unnamed related taxa such as DCM G10603 (Powell 1987; Benson and Barrett 2009). In contrast, other theropods, including the basal carcharodontosaurian *Neovenator* (Brusatte et al. 2008), more basal allosauroids (*Allosaurus*: Madsen 1976; *Sinraptor*: Currie and Zhao 1993), and ceratosaurids (Madsen and Welles 2000; Rauhut 2004) possess shallower plates. Because derived carcharodontosaurids lack a distinct maxillary anterior process, the anteromedial process in these taxa is located further dorsally relative to the interdental plates than in *Kelmayisaurus*. Therefore the combination of tall interdental plates and an anteromedial process that is close to the dorsal margin of the plates is known only in *Kelmayisaurus*.

Parts of six alveoli are preserved; the anterior four are essentially complete and the posterior two are heavily weathered. Complete alveoli have oval outlines, which are wider mesiodistally than labiolingually. A replacement tooth is present in the crypt for alveolus 4. This tooth is 70 mm long apicobasally, its mesial margin is strongly curved, and its distal margin is nearly straight ventrally, similar to the replacement teeth of many theropods. Unfortunately, surface details, such as the presence of enamel wrinkles (Brusatte et al. 2007), are difficult to discern due to erosion. The labial parapet of the alveoli, comprised of the lateral surface of the maxilla, extends much further ventrally than the lingual parapet, formed from the interdental plates. However, this may be an artefact of poor preservation.

Dentary.—The left dentary is well preserved, and only the anterior tip and the fragile, sheet-like portion immediately posterior to the tooth row are missing. The dentary is 523 mm in length and keeps a relatively constant dorsoventral depth along most of the tooth row, but expands in depth posterior to alveolus 13. The anterior end is expanded only slightly relative to the remainder of the tooth row, unlike the condition in derived carcharodontosaurids in which the anterior dentary is expanded and squared-off, primarily by the presence of a distinct "chin-like" anteroventral process (Fig. 2C; e.g., Novas et al. 2005; Coria and Currie 2006; Brusatte and Sereno 2007). An unexpanded anterior dentary is also seen in the basal neovenatorid carcharodontosaurian *Neovenator* (Fig. 2A; Brusatte et al. 2008). The dorsal margin of the tooth row is concave when seen in lateral view, whereas the ventral margin is convex anteriorly and concave posteriorly. The

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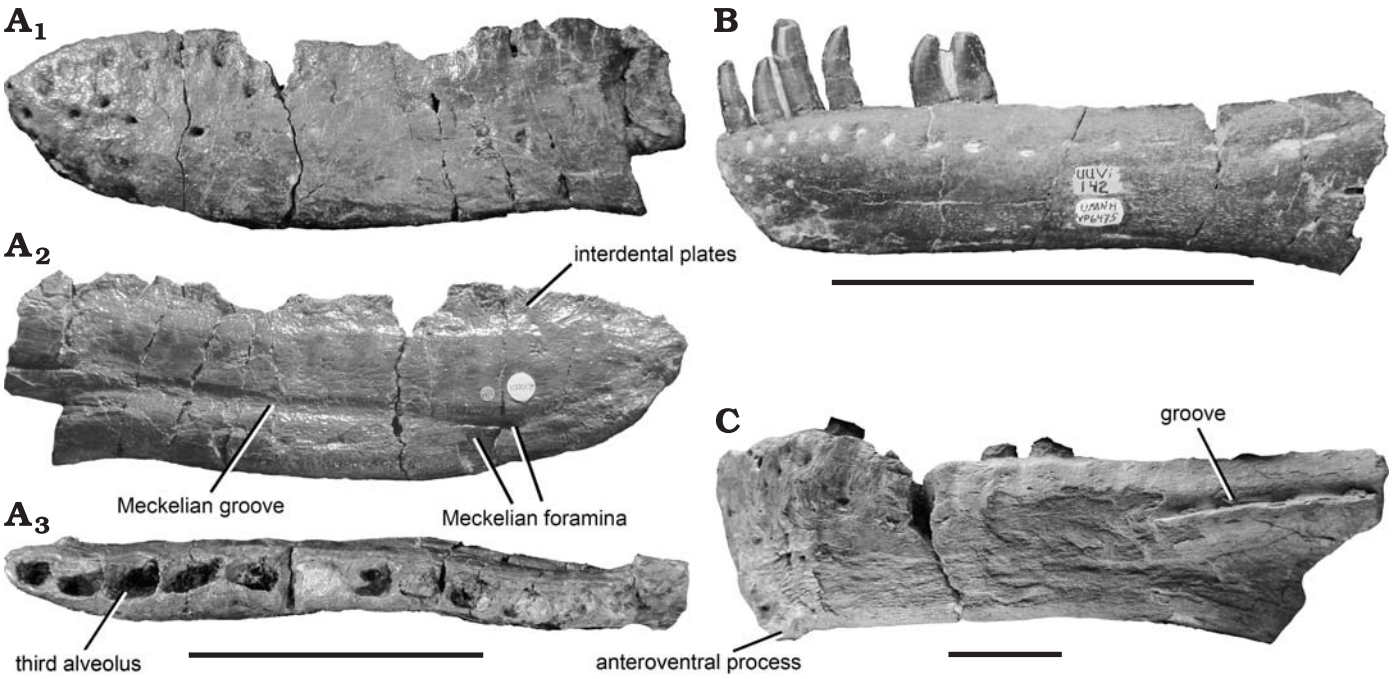


Fig. 2. Dentaries of allosauroid theropod dinosaurs. **A**. *Neovenator salerii* Hutt, Martill, and Barker, 1996, England, Wessex Formation, Lower Cretaceous (BMNH R10001). **B**. *Allosaurus fragilis* Marsh, 1877, United States, Morrison Formation, Upper Jurassic (UMNH VP 6475). **C**. *Giganotosaurus carolinii* Coria and Salgado, 1995, Argentina, Candeleros Formation, Upper Cretaceous (MUCPv-95). Photographs in lateral (A_1, B, C), medial (A_2), and dorsal (A_3) views. Scale bars 10 cm.

dorsal section of the posterior margin of the dentary, which would have been overlapped by the surangular, is nearly vertical for a short distance before sloping posteroventrally. This is also the case in other allosauroids (e.g., Madsen 1976), whereas abelisaurids (e.g., Sampson and Witmer 2007) and many coelurosaurs (e.g., Currie 1995) have posterior margins that are essentially straight dorsoventrally. Although the posterior part of the dentary is well preserved, there is no obvious concave margin for the external mandibular fenestra. Thus, if the dentary did border the fenestra, this contribution must have been small.

In dorsal view, the dentary is straight across its entire length, as in the carcharodontosaurians *Acrocanthosaurus* (NCSM 14345) and *Neovenator* (Fig. $2A_3$; Brusatte et al. 2008), as well as *Sinraptor* (Currie and Zhao 1993) and most other basal tetanurans. However, in derived carcharodontosaurids (*Carcharodontosaurus*: Brusatte and Sereno 2007; *Giganotosaurus*: Calvo and Coria 2000; *Mapusaurus*: Coria and Currie 2006), *Allosaurus* (Madsen 1976), *Piatnitzkysaurus* (PVL 4073), and abelisaurids (e.g., Sampson and Witmer 2007) the dentary curves anteromedially along its length to form a broad, U-shaped snout.

Original bone surface is present across most of the dentary, and the smooth lateral surface is especially well preserved. The primary neurovascular row is distinct. Anteriorly, the row is comprised of deep, circular foramina. There is approximately one foramen per alveolus, and these are located only 15 mm ventral to the alveolar margin. Posterior to the fourth alveolus the row curves ventrally, such that it is 25 mm ventral to the alveolar margin at the level of alveolus 6. Additionally, posterior to alveolus 8 the individual foramina are replaced by a dorsoventrally deep and strongly inset groove. The groove curves dorsally as it extends posteriorly, giving it a concave dorsal margin when seen in lateral view. However, as this curvature occurs in concert with the posterior expansion of the dentary, the groove is still located 25 mm ventral to the tooth row where it terminates. The primary groove is especially deep and well defined in *Kelmayisaurus*, similar to the condition in some megalosauroids (e.g., Rauhut 2003) and some carcharodontosaurids (Fig. 2C) but contrasting with the weaker grooves of most other theropods (Rauhut 2003). In *Allosaurus* and *Neovenator* a discrete groove is absent, and foramina are simply arrayed in a series (Fig. $2A_1$, B).

Two additional neurovascular features are present on the lateral surface. A ventral row of foramina, which are more ovoid than the primary foramina, is located along the ventral margin of the anterior dentary. These are present below the first four alveoli, and there is one foramen per alveolus. Additionally, there is a pronounced groove anteriorly, anterior to alveolus 5. This groove is 74 mm in length and curves dorsally as it continues posteriorly, eventually becoming confluent with the primary groove at the level of alveolus 6. Within this groove are four deep foramina, which decrease in size posteriorly. This groove is not present in other basal tetanurans (Fig. 2; e.g., Madsen 1976; Currie and Zhao 1993; Allain 2002), and is thus considered an autapomorphy of *Kelmayisaurus*.

The medial surface of the dentary is well preserved. The symphysis is nearly flat and poorly-defined, not bulbous and rugose as in derived carcharodontosaurids (Brusatte and Sereno 2007). However, an anterodorsally-inclined longitudinal ridge traverses the symphysis immediately ventral to midheight. This feature has been noted in megalosauroids

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(Benson 2008) and may be widespread among theropods. Ventral to the third alveolus are two Meckelian foramina; both are ovoid, equal in size, and one is located anterodorsal to the other. The Meckelian groove is shallowly inset where it meets the foramina, but becomes more deeply inset and taller dorsoventrally as it continues posteriorly. Ventral to alveolus 13 the groove is marked by a distinct step where it meets the adductor fossa; ventral to this step is a rectangular notch for the splenial articulation. The groove extends anteroventrally and its dorsal margin is better defined than its ventral margin. It is bordered dorsally by the lingual bar, which is deepest anteriorly above the Meckelian foramina. The bar tapers in depth posteriorly until the level of alveolus 9, from which point it maintains a constant depth. It also becomes more robust posteriorly, in concert with the progressively more inset Meckelian groove. The bar is bordered dorsally by the paradental groove, above which the interdental plates are fused into a single lamina across the first 11 alveoli. The posterior-most three alveoli are small, triangular, and unfused. No tooth replacement foramina are clearly visible.

Fifteen alveoli are clearly visible, and there was likely a 16th alveolus that is missing at the broken anterodorsal corner of the dentary. All alveoli are suboval in dorsal view and much longer mesiodistally than labiolingually. Even the second and third alveoli are suboval, unlike the situation in many megalosauroids (e.g., Charig and Milner 1997; Allain 2002; Sadleir et al. 2008) and *Acrocanthosaurus* (NCSM 14345), in which the anterior three alveoli are subcircular and the third is relatively enlarged compared to the other alveoli. The third dentary alveolus of *Neovenator* is also relatively enlarged (Fig. 2A$_3$). In *Neovenator* the alveoli are subrectangular, similar to the condition in abelisaurids (e.g., Sereno et al. 2004) but unlike all other basal tetanurans. No erupted or replacement teeth are clearly preserved in *Kelmayisaurus*, but the labiolingually thin alveoli may suggest that the teeth were transversely compressed, as in some derived carcharodontosaurids (Sereno et al. 1996).

Discussion

Body size of the holotype.—Estimating the body size of the *Kelmayisaurus* holotype is difficult, as all of the appendicular bones commonly used as size or mass proxies are missing. However, Currie (2003a) reported that skull length and femur length are approximately isometric in another clade of large theropods, the tyrannosaurids. Thus, a reasonable body length estimate may be obtained by comparing the length of the dentary to that of other theropods. The dentary of *Kelmayisaurus* is 523 mm long, slightly larger (approximately 5%) than typical adult individuals of *Allosaurus* (e.g., Madsen 1976). Thus, to a first approximation, *Kelmayisaurus* can be considered as approximately the same body length and mass as *Allosaurus*, which is estimated to have reached masses of 1620 kg and body lengths of 10–12 m (Christiansen and Farina 2004). This is much larger than the estimated body size of the younger Asian carcharodontosaurid *Shaochilong*, which has a maxilla that is only 75% the length of that of *Allosaurus* (Brusatte et al. 2009a).

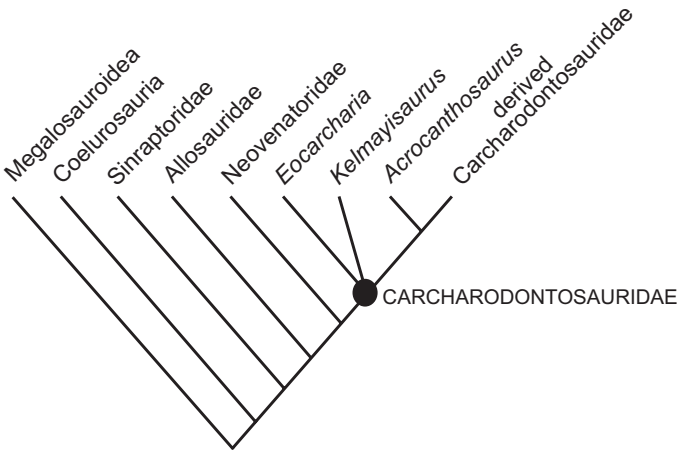


Fig. 3. The phylogenetic relationships of *Kelmayisaurus* and other basal tetanuran theropods. Strict consensus of 1728 most parsimonious trees (639 steps) recovered by the cladistic analysis (CI = 0.44; RI = 0.64). "Derived carcharodontosaurids" include *Shaochilong*, *Tyrannotitan*, *Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus*. *Kelmayisaurus* is recovered as a basal member of Carcharodontosauridae.

Systematic affinities of *Kelmayisaurus*.—To test the phylogenetic position of *Kelmayisaurus*, we added it to the cladistic data matrix of Benson et al. (2010) (Appendix 1). When analyzed with the same search strategy described by Benson et al. (2010), the new analysis recovered 1728 most parsimonious trees (MPTs) with a length of 639 steps, a consistency index (CI) of 0.44, and a retention index (RI) of 0.64 (strict consensus presented in Fig. 3). As in the initial analysis of Benson et al. (2010), Megalosauridae and Megaraptora were poorly resolved in the strict consensus due to a small number of wildcard taxa. Most important, however, *Kelmayisaurus* was recovered as a basal carcharodontosaurid in all MPTs, and in the strict consensus it falls into a polytomy with *Eocarcharia* and a clade comprising *Acrocanthosaurus* and all more derived carcharodontosaurids. Therefore, we refer *Kelmayisaurus* to Carcharodontosauridae, and regard it as a basal member of the clade. We note that, after deletion of the wildcard taxon *Poekilopleuron*, one additional step allows *Kelmayisaurus* to be recovered (i) within Allosauroidea as the sister taxon of Neovenatoridae + Carcharodontosauridae; (ii) within Megalosauridae as the sister taxon of *Megalosaurus bucklandii* + *Torvosaurus tanneri*; or (iii) within Coelurosauria as the sister taxon of *Guanlong*, *Tanycolagreus*, or *Tanycolagreus* + *Guanlong*. Thus, the fragmentary nature of the *Kelmayisaurus* holotype, coupled with homoplasy in the phylogenetic analysis, renders weak support for a carcharodontosaurid affinity.

With this being said, a carcharodontosaurid referral is also supported by a careful review of characters and compar-

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isons to other theropods. *Kelmayisaurus* possesses maxillary interdental plates that are more than twice as tall dorsoventrally as they are wide anteroposteriorly, a feature only found in carcharodontosaurids such as *Acrocanthosaurus* (NCSM 14345) and *Carcharodontosaurus* (Brusatte and Sereno 2007) and the megalosaurids *Megalosaurus* (Benson 2010) and *Torvosaurus* (Britt 1991). In contrast, plesiomorphically short plates are present in the closest carcharodontosaurid outgroups (e.g., *Neovenator*: Brusatte et al. 2008). Tall interdental plates were recovered as a synapomorphy of a clade of derived carcharodontosaurids (equivalent to Carcharodontosauridae sensu Benson et al. 2010) by Brusatte and Sereno (2008) and Brusatte et al. (2009a). However, *Kelmayisaurus* lacks many other distinctive features of derived carcharodontosaurids (i.e., *Acrocanthosaurus*, *Carcharodontosaurus*, *Giganotosaurus*, *Mapusaurus*, *Shaochilong*), including a pronounced anteroventral process ("chin") of the dentary and rugose craniofacial bones (which are absent in some carcharodontosaurids, including *Acrocanthosaurus*: Currie and Carpenter 2000). This character review, therefore, is congruent with the phylogenetic analysis in suggesting that *Kelmayisaurus* is a basal carcharodontosaurid that falls on the line towards more derived members of the clade. This phylogenetic position is consistent with the Early Cretaceous age of *Kelmayisaurus*, as most derived carcharodontosaurids are younger than Albian in age, the youngest possible age for the Lianmugin Formation.

The presence of fused interdental plates is also consistent with derived allosauroid affinities, as this feature is seen in *Allosaurus* (Madsen 1976) and carcharodontosaurians (e.g., Fig. $2A_2$; Sereno et al. 1996). This was also derived independently in ceratosaurs (Madsen and Welles 2000; Carrano and Sampson 2008) and the megalosaurid *Torvosaurus* (Britt 1991). Nevertheless, *Kelmayisaurus* is unlikely to pertain to a derived megalosauroid (Megalosauridae or Spinosauridae) because it lacks a unique synapomorphy of the clade comprising these two families: a paradental groove that is wide anteriorly, defining a distinct gap between the interdental plates and the medial wall of the maxilla (Benson 2008, 2010; Benson et al. 2008). Additionally, many megalosauroids, including *Torvosaurus* (Britt 1991), possess an expanded, subcircular third dentary alveolus, which is not present in *Kelmayisaurus*.

Kelmayisaurus is also not likely to be a ceratosaur: it lacks the external bone texturing of derived abelisaurids (e.g., Sampson and Witmer 2007); possesses a prominent anterior process of the maxilla (absent in ceratosaurs, Rauhut 2003); has a more steeply posteroventrally inclined dorsal margin of the posterior dentary compared to the more dorsoventrally straight profile of abelisaurids (Sampson and Witmer 2007), noasaurids (Carrano et al. 2002), and ceratosaurids (Madsen and Welles 2000); has a deeper and more pronounced primary neurovascular groove on the dentary than in noasaurids (Carrano et al. 2002) and abelisaurids (Sampson and Witmer 2007); has a primary neurovascular groove located closer to the tooth row than in ceratosaurids (Madsen and Welles 2000) and abelisaurids (Sampson and Witmer 2007); and does not have the characteristic expanded anterior dentary and heterodont dentition of the best-known noasaurid, *Masiakasaurus* (Carrano et al. 2002).

Finally, *Kelmayisaurus* is unlikely to be a large-bodied coelurosaur. The interdental plates are fused and the anterior dentary is rounded, unlike the condition in tyrannosaurids in which the plates are unfused and the anterior end of the dentary is straight and slopes posteroventrally (e.g., Brochu 2003; Currie 2003b; Brusatte et al. 2009b). Dromaeosaurids possess dentaries with a more anterodorsally-straight posterior margin, a weaker and less defined primary neurovascular groove, and Meckelian foramina that are positioned far apart (not adjacent to each other), as well as maxillae with shallower interdental plates (e.g., Currie 1995; Norell et al. 2006). Other coelurosaur groups with known large-bodied members can easily be distinguished from *Kelmayisaurus* by their peculiar skulls, which are often edentulous and clearly modified for a diet that is not primarily based on procuring large prey (e.g., Xu et al. 2007).

Implications of the carcharodontosaurid affiliation of *Kelmayisaurus*.—*Kelmayisaurus* represents the second known Asian carcharodontosaurid. Carcharodontosaurids were originally discovered in Africa (Stromer 1931) and later in South America (Coria and Salgado 1995), and were once considered to be an endemic Gondwanan clade (e.g., Currie and Carpenter 2000; Allain 2002; Novas et al. 2005). The reinterpretation of *Acrocanthosaurus* as a carcharodontosaurid (Sereno et al. 1996; Harris 1998), along with the discovery of the British *Neovenator* (Hutt et al. 1996) and more recently the Spanish *Concavenator* (Ortega et al. 2010), suggests that carcharodontosaurids and their immediate relatives instead represent a global radiation. However, until the recent redescription of *Shaochilong* (Brusatte et al. 2009a) there was no strong evidence that these giant predators inhabited Asia.

The identification of *Kelmayisaurus* as a carcharodontosaurid not only adds further evidence that this clade inhabited Asia, but also suggests that carcharodontosaurids were present in Asia for a lengthy period of time. *Shaochilong* is from ca. 92 Ma rocks (Turonian), making it the youngest unequivocal carcharodontosaurid (Brusatte et al. 2009a). The age of the Lianmugin Formation, the rocks entombing the holotype of *Kelmayisaurus*, is not known with certainty, but falls somewhere within the Valanginian to the Albian (i.e., ca. 140–99.6 Ma). There is no evidence that *Kelmayisaurus* and *Shaochilong* belong to the same subclade or lineage, but the presence of two carcharodontosaurids separated by at least 8 Myr indicates that these large predators may have been a common and long-lived component of Early–mid Cretaceous terrestrial ecosystems in Asia. Indeed, the Asian carcharodontosaurid record now eclipses that of North America and Europe, both of which have yielded only a single carcharodontosaurid taxon. Emerging evidence, therefore, strongly supports a global radiation of carcharodontosaurids within the large-predator niche during the Early–mid Cretaceous.

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Acknowledgements

We thank Thomas Holtz (University of Maryland, College Park, Maryland, USA) and Philip Currie (University of Alberta, Edmonton, Canada) for their helpful reviews, and SLB thanks David Hone and Corwin Sullivan (both Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) for access to specimens and hospitality during his visit to Beijing. We thank many curators for access to specimens in their care, foremost Alejandro Kramarz (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina), Juan Canale (Museo Municipal Ernesto Bachmann, El Chocon, Argentina), Jorge.Calvo (Centro de Investigaciones Paleontológicas Lago Barreales, Neuquen, Argentina), Sandra Chapman (The Natural History Museum, London, UK), Richard Cifelli (Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA), Rodolfo Coria (Museo Carmen Fuenes, Plaza Huincul, Argentina), Mike Getty (Utah Museum of Natural History, Salt Lake City, Utah, USA), Steve Hutt (Dinosaur Isle Museum, Sandown, UK), Martin Munt (Dinosaur Isle Museum, Sandown, UK), Jeff Person (Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA), Paul Sereno (University of Chicago, Chicago, Illinois, USA), Vince Schneider (North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA), and Xijin Zhao (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China). SLB is supported by a National Science Foundation Graduate Research Fellowship and Doctoral Dissertation Improvement Grant (NSF DEB 1110357), and his visit to China was supported by the American Museum of Natural History, Division of Paleontology (administered by Mark Norell). RBJB's research is supported by a fellowship at Trinity College, Cambridge and Leverhulme Foundation grant RPG-129. XX is supported by the Chinese Academy of Sciences and the National Natural Science Foundation of China.

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Appendix 1

Scores of *Kelmayisaurus* for the phylogenetic dataset of Benson et al. (2010):

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